BIBLIOGRAPHY ON METHODS OF ANALYZING BIRD BANDING DATA

With Special Reference to the Estimation of Population Size and Survival

UNITED STATES DEPARTMENT OF THE INTERIOR
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Introduction

Many methods for estimating parameters of natural populations have been proposed since the turn of the century. Publications describing these methods are widely scattered and often difficult to comprehend. Furthermore, workers in different fields--e.g., fisheries, entomology, ornithology--have often developed and used their own methods, and there has been little interchange of theory, methodology, or necessary assumptions between these fields of research.

This bibliography is an effort to bring together references from various sources relating to methods that have application or at least historical interest and background in the analysis of bird banding experiments. Several papers reviewing methods or assumptions are included. Attention is focused on the estimation of population size and survival using some type of capture-recapture method. A number of papers dealing with methods of estimating band reporting rates, immigration and mean life span are also included. In the newer, more general models, there is no essential difference between recoveries from dead birds (single-recapture experiments) and live returns or retraps (multiple-recapture experiments) (Jolly, 1965; Cormack, 1968). Both types of experiment are merely sampling procedures and they have several basic similarities. The term *recapture* is descriptive of the general process of interest.

Although bird banding is an expensive and time-consuming effort, insufficient attention has often been given to planning the study, assessing the assumptions, and analyzing the data thoroughly. The literature emphasizes the need for detailed planning of banding operations before the field work is started (DeLury, 1947, 1951; Orians, 1958). Data gathering and data analysis should be coordinated through proper planning and realistic evaluation of the necessary assumptions. Planning is crucial if the study is to produce accurate and precise estimates of population parameters. As DeLury (1954) pointed out, "...it is an expensive impropriety to maintain that an untrustworthy estimate is better than none."

Cormack (1968) provides an excellent review of the literature on methods relating to capture-recapture studies. Seber's (1972a) book treats the subject at length and is the most comprehensive and unifying publication available. Taylor (1966) discusses some of the methods most relevant to the bird population studies, and Seber (1972b) reviews methods used in bird banding experiments and notes problems with most of the methods currently in use in ornithological work.

Much of the literature on capture-recapture methods is difficult to read because of the extensive use of mathematical statistics in this field. Biologists are referred to Kendall and Buckland: (1970. A dictionary of statistical terms. Hafner, N.Y.) for definitions of statistical terms.

Current Methods

At present, there are a number of efficient and realistic methods available for the analysis of bird banding experiments. Although not a complete list, the following papers describe methods that warrant serious consideration in the analysis of bird banding experiments: Chapman (1961), Chapman and Robson (1960), Cormack (1964), Darroch (1958, 1959, and 1961), Eberhardt (1969a), Fisher and Ford (1947), Jolly (1963, 1965, 1971), Manly (1969), Manly and Parr (1968), Paulik (1963), Paulik and Robson (1969), Robson (1963 and 1969), Robson and Chapman (1961), and Seber (1962, 1965, 1970a, 1971). Of these, the papers by Cormack (1964), Darroch (1961), Jolly (1965, 1971), Manly and Parr (1968), Robson (1969), and Seber (1965, 1970a, 1971), are a good reflection of the "state of the art" of methods for the general capture-recapture experiment in which a minimum of assumptions are necessary. Several of the methods above are special cases of, or closely related to, the general theory presented independently in 1965 by Jolly and Seber.

Deterministic and Stochastic Models

A fundamental difference exists between deterministic and stochastic methods for the analysis of capture-recapture experiments. In the deterministic model, the population is regarded as being subject to a survival rate of *exactly* ϕ_i, say, during the interval between the i and $i+1^{th}$ sample. Stochastic models treat ϕ_i as the *probability* of an animal surviving the interval between the i and $i+1^{th}$ sample. As Jolly (1965: 226) explains, this is the essential difference between the deterministic and stochastic models. It is clear that the stochastic model is the more realistic of the two.

Early workers developed methods for estimating population parameters along deterministic lines (Bailey, 1951, 1952; Fisher and Ford, 1947; Jackson, 1933, 1937, 1939, 1940, 1948; and others), while more recent efforts have focused much-needed attention on stochastic models. Early methods considered only closed populations, while more recent methods

allow for immigration and emigration or death. Current methods often allow estimates of both population size and survival (as well as immigration, reporting rate, and possibly mean life span), while earlier methods treated these problems separately. The estimation of the variance of parameter estimates is an extremely important aspect of population studies and has received increased attention in the last two decades.

The deterministic model developed by Jolly (1963) seems to be the most satisfactory model of its type. However, there appear to be definite and important advantages in using the newer, more general, and realistic stochastic theory rather than the earlier, deterministic theory. Jolly (1965:235) concludes:

> As deterministic assumptions were originally introduced into capture-recapture problems in an attempt to simplify the theory, there now remains no good reason for their retention. It is therefore recommended that, for capture-recapture problems in general, purely deterministic models, with their approximations and limitations, be abandoned in favour of stochastic models.

Cormack (1968) agrees, and maintains that deterministic models have been superseded by stochastic models.

Efforts toward stochastic models began in the early 1950's in a series of papers by Leslie and his colleagues. The theory was advanced considerably in papers by Darroch (1958, 1959); he provided the basic theoretical framework for much of the recent research on methods. Important stochastic models were presented in the early 1960's by Cormack (1964), Robson (1963), and Seber (1962). In 1965, Jolly and Seber provided fully stochastic models and gave explicit estimates for several parameters of interest and their respective variances. Although the stochastic methods of Jolly (1965) and Seber (1965) are similar in several respects, Jolly's is the more general in that losses on capture (either intentional or accidental) are allowed. This is important in banding experiments with small song birds. Jolly's theory is also more general, in that he developed a probability model for heterogeneous populations where certain classes of animals behave in different ways. However, he provides estimates only for homogeneous populations, since explicit estimates could not be found for several heterogeneous classes (e.g., age-dependent survival classes).

Although there are a number of powerful methods for the analysis of bird banding experiments, the problem of age-dependent survival rates is still largely extant. The proper estimation of survival rates for birds banded as juveniles continues to present a particularly thorny problem. A number of life table methods for estimating age-dependent survival rates were proposed in the early 1950's (Farner, 1955; Haldane, 1953, 1955; and Hickey, 1952). These methods are still in fairly common use because more adequate methods have not appeared until very recently. The recent methods still leave much to be desired concerning realistic assumptions (e.g., variable reporting rates), and are often inefficient.

Hammersley (1953) investigated estimation methods for age-dependent populations, but, according to Darroch (1959), his paper contains an error in the likelihood function. Manly and Parr (1968) described a method useful for estimating age-dependent survival rates for multiple-recapture experiments; however, it is inefficient and therefore sensitive to small samples. Since then, Manly (1969, 1971a) has extended the theoretical aspects and provided variance estimates for the parameters. Simulation experiments by Manly (1970) suggest that this method is satisfactory for populations with a high degree of age-dependency. Cormack (in Fordham, 1970) and Seber (1971) have recently developed maximum likelihood methods for estimating age-dependent survival rates but these methods necessitate the assumption of a constant reporting rate. Further work on this important problem is clearly needed.

Theory

Many of the most promising methods are based on a general probability model consisting of products of multinomial distributions or conditional binomial distributions. The Poisson, geometric, hypergeometric, exponential, and other distributions have also been used. Recently, Robson (1969) suggested that a negative binomial distribution may be more appropriate than the others. The powerful stochastic methods produced in the last 14 years, as well as many of the earlier methods, have been developed primarily from the theory of maximum likelihood. In many cases, explicit estimation equations are found, often with some loss of efficiency, and computational effort is fairly easy and straightforward. In other cases, equations must be solved iteratively for the parameter estimates of interest, and computational difficulties arise without a high-speed computer.

Estimators developed from the theory of maximum likelihood have many good statistical properties but assume reasonably large samples are available for analysis. "Large" is not well defined in practice, but certainly the analysis of experimental results involving only a dozen total recaptures is not warranted.

Iterative Solutions

The ability to obtain explicit estimates of parameters seems increasingly limited as the model becomes more general and realistic. Cormack (in Fordham, 1970) suggested that a model which allowed survival to vary with calendar year as well as with age could be estimated by maximum likelihood using numerical methods and a digital computer. Estimates of survival rates and their variances and other parameters could be estimated in this manner; however, computer time required increases sharply with the number of parameters in the model. Iterative methods are more complex, nearly always require a computer for solution, and can be expensive because of the computer time required. Despite these disadvantages, I believe methods requiring an iterative solution will become increasingly important in the analysis of data from large banding studies of immature or subadult birds. Furthermore, a measure of effort may be possible to incorporate into an iterative method. Models incorporating effort statistics are important and have been virtually ignored since Darroch (1958, 1959). Iterative methods in the analysis of capture-recapture experiments represent an important avenue of research, and at this time almost no literature has been published in this area. Papers describing iterative methods must be accompanied by computer routines if the methods are to see use by most bird banders and field biologists (see Roberts, 1971).

For the bird bander or field biologist, the primary drawback in the use of the newer techniques is likely to be their complexity. The theoretical basis of most of the better methods lies deep in the field of mathematical statistics. In most cases the use of a particular method is fairly straightforward, but the mathematical theory and derivatión of the various estimators are quite difficult. Fortunately, many authors have included examples illustrating the use of the methods they describe. However, it is important for the bird bander or field biologist to fully understand the methods, their assumptions and limitations. This suggests that a joint effort between biologists, bird banders, and ornithologists

on the one hand, and statisticians on the other, would be advantageous. White (1971a, 1971b) has developed a general computer program for Jolly's stochastic model. This allows fast, accurate, and inexpensive estimates to be made if the assumptions of Jolly's method have been met and the study has been properly planned and executed. White's work has particular importance to some of the large banding programs currently in progress.

Assumptions

A number of papers present methods to test the assumptions being made (Leslie et al., 1953; Leslie, 1958 [in Orians]; Carothers, 1971; Chapman and Robson, 1960; Cormack, 1966; Seber, 1962, 1965, 1970b). This is a very important area and one needing further research. Tests of the basic assumptions are of utmost importance. In particular, the estimates of variance of the parameters being estimated are highly dependent on the assumptions made about the probability model of the experiment. If the assumptions of the method are not met, the variance of the estimates will be incorrect.

Recently, several papers have presented the results of computer simulation experiments of capture-recapture techniques. These allow the assessment of the practicality of the approach, its robustness, and any problems with the techniques. Simulation studies by Eberhardt (1972) focus attention on a number of the simpler methods of estimating survival rates for closed populations. Of those studied, the Chapman-Robson (1960) method was clearly superior, although it necessitates a number of extremely restrictive assumptions. Simulation experiments by Manly (1970, 1971b) provide much-needed insight into the performance of several methods when subjected to hypothetical populations with various known characteristics. Too little has been attempted concerning alternatives if one of the important assumptions is not fully met. Burnham and Overton (1969), Fretwell (in prep.), Janion et al. (1968), Marten (1970), Seber (1970b), and Tanaka and Kanamori (1967) have presented methods to estimate parameters when members of the population are "trap happy" or "trap shy."

Suggested Reading

Anyone planning a banding study of a bird population may find the list of references in this bibliography somewhat bewildering. Although it is impossible to suggest a brief reading list for every conceivable banding experiment, the references suggested below may provide a reasonable starting point for many situations.

Background and Review Reading.--Cormack (1968), Seber (1972a, 1972b), and Taylor (1966) present comprehensive reviews of capture-recapture methods. The papers by Darroch (1958, 1959), Jolly (1963), Leslie and colleagues (1951, 1952, 1953), and Seber (1962) are relevant background reading.

Methods.--Cormack (1964, 1970 [in Fordham]), Darroch (1961), Jolly (1965, 1971), Manly and Parr (1968), Manly (1969), Robson (1969), and Seber (1965, 1970a, 1971, 1972a).

Tests of Assumptions.--Carothers (1971), Cormack (1966), Leslie (1953, 1958 [in Orians]), Manly (1971a), and Seber (1962, 1965, 1970b).

If the population under study is closed and several restrictive assumptions can reasonably be made, the following references should be consulted: Chapman (1954, 1961), Chapman and Robson (1960), Eberhardt (1969a), Paulik (1963), Paulik and Robson (1969), and Robson and Chapman (1961).

Summary

In summary, several points could be emphasized. Bird banding experiments must be developed on a scientific basis if accurate and precise results are to be expected. Planning the project and reviewing the literature should certainly precede the field work. Estimates of various population parameters are not made easily and should not be made casually. Assumptions underlying the method of analysis to be used should be fully recognized. The newer stochastic models have a number of important advantages and are therefore recommended. Methods of calculating the variance of population parameters are of great importance in bird banding experiments. Estimates of population parameters--made after years of expensive field work--that have extremely wide confidence intervals usually represent wasted time and money. Several satisfactory techniques are available for the analysis of bird banding experiments for adult birds. Methods for age-dependent survival rates are still in the developmental stages and represent a serious gap as far as ornithological work is concerned. Bird banding experiments are highly variable and depend on a number of factors. No one method will be appropriate for all cases.

Acknowledgments

Although this bibliography contains nearly 200 references, it is probably not complete; however, I believe that it includes most of the important papers. I wish to thank R. M. Cormack, G. M. Jolly, B. J. F. Manly, G. A. F. Seber, and E. G. White for sending me reprints and literature citations for this paper. J. P. Rogers provided editorial assistance.

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